

- ELIOT, J. M., ed., 1978. *The butterflies of the Malay Peninsula*, 3rd ed. Kuala Lumpur, Malaysia, Malayan Nature Society: xiv + 578 pp., 35 pls.
- FERRIS, C. D., 1976. Book review. *J. Lepid. Soc.*, 30:138-143.
- _____, & J. F. EMMEL, 1982. Discussion of *Papilio coloro* W. G. Wright (= *Papilio rudkini* F. & R. Chermock) and *Papilio polyxenes* Fabricius. *Bull. Allyn Mus.*, (76): 13 pp.
- FORBES, W. T. M., 1960. *Lepidoptera of New York and neighboring states. Agaristidae through Nymphalidae including butterflies*. Part 4. Ithaca, N. Y., Cornell Univ. Agr. Expt. Sta., Mem. 371: 188 pp.
- GOULD, S. J., 1982. The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution. in Milkman, R. (ed.), *Perspectives on evolution*: pp. 83-104.
- _____, & N. ELDREDGE, 1977. Punctuated equilibrium: the tempo and mode of evolution reconsidered. *Paleobiology*, 3:115-151.
- HOLLAND, W. J., 1931. *The butterfly book* (rev. ed.). Garden City, N. Y., Doubleday Doran & Co.: xii + 424 pp., 77 pls.
- HOVANITZ, W., 1962. *Argynnis* and *Speyeria*. *J. Res. Lepid.*, 1:94-95.
- _____, 1965 ["1964"]. Book review. *J. Res. Lepid.*, 3:18.
- HOWE, W. H. (ed.), 1975. *The butterflies of North America*. Garden City, N. Y., Doubleday & Co.: xiii + 633 pp., 97 pls.
- HUEBNER, J., [1819]. *Verzeichniss bekannter Schmettlinge* [sic.]. [part 7]. Augsburg, Priv. publ.
- LINDSEY, A. W., JR., E. L. BELL & R. C. WILLIAMS, JR., 1931. The Hesperioidea of North America. *Denison Univ. Bull. Sci. Lab.*, 26:1-142.
- MILLER, L. D., & F. M. BROWN, 1979. Studies in the Lycaeninae (Lycaenidae). 4. The higher classification of the American coppers. *Bull. Allyn Mus.*, (51); 30 pp.
- _____, 1981. A catalogue/checklist of the butterflies of America north of Mexico. *Mem. Lepid. Soc.*, (2): vii + 280 pp.
- MUNROE, E. G., 1961. A classification of the Papilionidae (Lepidoptera). *Canadian Ent.*, suppl. 17:1-51.
- dos PASSOS, C. F., 1964. A synonymic list of the Neactic Rhopalocera. *Mem. Lepid. Soc.*, (1): v + 145 pp.
- _____, & L. P. GREY, 1947. Systematic catalogue of *Speyeria* (Lepidoptera: Nymphalidae) with designations of types and fixations of type localities. *American Mus. Novitates*, (1370): 30 pp.
- RAUP, D. M., 1978. Cohort analysis of generic survivorship. *Paleobiology*, 4:1-15.
- SCUDDER, S. H., 1875. Synonymic list of the butterflies of North America, north of Mexico. Part 1, Nymphales. *Bull. Buffalo Soc. Nat. Sci.*, 2:233-269.
- SIBATANI, A., 1974. A new genus for two new species of Lycaeninae (s. str.) (Lepidoptera: Lycaenidae) from Papua-New Guinea. *J. Australian Ent. Soc.*, 13:95-110.
- SKINNER, H., 1898. *A synonymic catalogue of the North American Rhopalocera*. Philadelphia, American Ent. Soc.: xvi + 99 + xiv pp.
- STANLEY, S. M., 1979. *Macroevolution: pattern and process*. San Francisco, W. H. Freeman Co.: xii + 332 pp.
- STRECKER, F. H. H., 1876 [1872-1878]. *Lepidoptera, rhopaloceres and heteroceres, indigenous and exotic; with descriptions and colored illustrations*. Reading, Pennsylvania, priv. publ.: 143 pp., 15 pls.
- WILSON, E. O., & W. L. BROWN, JR., 1953. The subspecies concept and its taxonomic application. *Syst. Zool.*, 2:97-111.

Nomenclature, Taxonomy and Evolution

Paul R. Ehrlich

and

Dennis D. Murphy

Department of Biological Sciences, Stanford University, Stanford, CA 94305

This response to Miller and Brown (1983) will have to be relatively brief, since we do not have room here to teach elementary courses in systematics or evolution. Miller and Brown seem to be under the impression that we were critical of their taxonomy, as the title of their paper—"Butterfly Taxonomy, A Reply"—indicates. On the contrary, as the title and content of our original paper (Ehrlich and Murphy, 1982) show, we were critical of the *nomenclature* they used, not the *taxonomy*. They thus miss the entire point of our critique, because nomenclature is not taxonomy, and certainly not biology! In his basic text *Principles of Systematic Zoology*, Ernst Mayr (1969, pp. 407 and 413) defines nomenclature as "a system of names" and taxonomy as "the theory and practice of classifying organisms." He further points out (p. 297):

"It is the role of nomenclature to provide labels for taxa at all levels, in order to facilitate communication among biologists. The scientific names for species of organisms and for the higher taxa in which they are placed form a system of communication, a language; they must fulfill the same basic requirements as any other language."

Mayr's three outstanding attributes for scientific nomenclature are uniqueness, universality, and stability. Of the latter he says (p. 298):

"As recognition symbols the names of objects would lose much of their usefulness if they were changed frequently and arbitrarily. It would surely create confusion if we were to call an object a spoon today but an apple next week. Yet this basic principle of communication has been constantly violated by zoologists. Altogether too much name changing has occurred in zoological taxonomy during the past 200 years."

Similar sentiments are found in the other standard source, George Gaylord Simpson's *Principles of Animal Taxonomy* (1961). For example, he makes the following point with emphasis (p. 112):

"A published classification in current use should be changed when it is definitely inconsistent with known facts and accepted principles, but only so far as necessary to bring it into consistency."

A nomenclature can remain relatively conservative to facilitate communication while the underlying classificatory system can be more fluid to represent, at best partially, better understanding of relationships. But, as Simpson admonishes, there should be strong reasons even for changing the taxonomy, let alone the nomenclature.

In this context, the notion that we were recommending "censorship" in proposing to stick to names in Howe unless there were reasons (clear polyphyly, highly distorted balance) for not so doing is seen as preposterous. Standardization is routine in scientific discourse. If Miller and Brown submitted to *Science* or any other refereed scientific journal an article that contained measurements in chains, rods, bushels, or pecks it would be rejected until those measurements were replaced with their metric equivalents. Would that be censorship??

We cannot help but note in passing, in terms of "censorship" that the Journal of the Lepidopterists' Society refused to publish our original manuscript on the novel grounds that the Society had published Miller-Brown. This refusal was surely a "first" for purportedly scientific journals, the rest of which routinely publish critiques of their previous articles. Furthermore the society is now going to require that all contributors to its season summary follow Miller-Brown nomenclature (*News of the Lepidopterists' Society*, Sept/Oct 1982, p. 62), even though a major segment of the society (see acknowledgments to Ehrlich and Murphy, 1982)—in fact, if our sample is representative, the vast majority of its members—think that nomenclature a disaster.

Some specific replies:

1. Catalogues are not the place to put unexplained new taxonomic arrangements.

2. There are no "overlooked" genera; most of the ones resurrected in Miller-Brown were correctly long-ignored.

3. The "no new names" issue begs the question. Names dredged out of synonymy where they have properly resided for a century and a half are operationally "new."

4. Generally the notes in Miller-Brown are utterly inadequate to justify the nomenclatural changes, since they do not deal with crucial issues of polyphyly or balance. For many of the more egregious choices, such as the resurrection of *Pterourus*, no explanation is given there at all. In others they follow nomenclaturally incompetent "revisions," for instance, accepting "*Occidryas*" even though Higgins (1978) gives no valid reason for proposing it as a genus.

5. Not using a name does not mean it will be "expunged from the literature."

6. Miller and Brown nicely summarize all of the reasons that their nomenclature *should be* rejected in the section "The usual objections... biological purpose." Hovanitz' (1964) objection to the splitting of *Speyeria*

from *Argynnis* is perfectly valid—we have not suggested going back simply because *Speyeria* has now become widely accepted. Hovanitz' other comments show how prescient he was about the downhill slide of butterfly nomenclature.

7. Nowhere did we "suggest" that the division of *Papilio* was based on genitalia—our only reference to genitalia was to the dependence upon them at the *specific level*. Miller and Brown now justify the nomenclatural inflation primarily on the basis of food plant differences. Their main criterion is that "*Papilio*" feeds on Umbelliferae, "*Heraclides*" on Rutaceae, and "*Pterourus*" on lauraceous plants. But "*Heraclides*" is also on Piperaceae, "*Papilio*" is commonly also on Rutaceae and Compositae in addition to Umbelliferae, and "*Pterourus*" feed on many families (*Papilio glaucus* and *P. rutulus* are recorded from at least 15 families) including Rutaceae! The correct interpretation of Berenbaum (a she not a "he") is not that natural groupings of swallowtails feed on natural groupings of plants, but that certain swallowtails are highly catholic in their choice of oviposition plants, as long as the plants share a similar chemical stimulant.

But even if different subgenera or species groups *did* feed exclusively on different groups of plants, that, in itself, is not an excuse for raising them to generic status. The subtleties of the factors governing larval host plant use by butterflies are just beginning to be elucidated (e.g., Chew, 1977; Holdren and Ehrlich, 1982; Lincoln, et al., 1982; Murphy, 1983; Rausher, 1982; Singer, 1972; Wiklund, 1982). Taxonomic affinity of the plants is just one such factor, and in many cases a minor one to boot (Janzen, 1979). *Celastrina argiolus* is known to feed on at least 18 plant families and *Strymon melinus* on 28. Will the next nomenclatural epic fraction them into 18 and 28 genera respectively?

The basic point, of course, recognized by all well-trained taxonomists, is that *levels* of genera, subgenera, etc. are biologically purely arbitrary, and that the use of genera should therefore be conservative to aid in communication (Mayr, 1969, p. 239). In addition, reclassification of *Papilio* does not remotely meet Simpson's criterion—there are no "known facts and accepted principles" that are violated by retaining *Papilio* in the sense that it has been used for the past few decades. The bottom line is that even the discovery of natural groups within *Papilio* would not *in itself*, be a reason to split the genus and change hundreds of names. Polyphyly or severe imbalance would be such a reason, but unless one or the other can be clearly demonstrated, taxonomic structure within *Papilio* should be recognized by subgenera or species groups.

Additionally, we must note Miller and Brown's story about *Papilio polyxenes coloro*. Although it has no direct relevance to the issue under discussion, it highlights how casual speculation in the literature gets translated into fact. Ferris and Emmel (1982) present not one shred of

evidence bearing on whether *P. zelicaon* did, does, or can "outcompete" *P. p. coloro*—nor do they claim to. Such evidence would be of enormous interest to the ecological and evolutionary communities as a whole, as competitive exclusion has never been demonstrated in herbivorous insects.

8. Large, uniform genera should not be broken up just because they are large—quite the opposite. And to fractionate small, uniform genera such as *Euphydryas* (12 species) is absurd. What possibly could be gained by dividing it in four?

9. Consistent application of subgenera does not mean burdening communication with them if there is no need. The genius of the Linnean system of binomial nomenclature is its parsimony—it avoids the older system of using an entire phrase to denote an organism. The idea is to maximize communication while restricting oneself to a two-part name.

10. Nomenclature that is "recognized by specialists" is, especially in groups like the butterflies where many specialists have extremely narrow training (or none at all), almost invariably oversplit. Rare is the specialist who considers broad balance in his or her application of names. One result of this is a continual shifting of names, often accompanied—as in the Miller-Brown catalogue—by no significant advance in understanding of the organisms. Continual name-changing, we repeat, is the major reason why most biologists consider taxonomy a non-science. Taxonomy is too important to evolutionary and ecological biology to destroy its reputation to please those who confuse manipulating names with science.

11. We are glad to be told that evolution is a *dynamic process*. Miller and Brown might like to be informed that everything they say in the three paragraphs that start "It cannot be questioned that evolutionary problems. . ." and end ". . . classification or phylogeny." is gibberish, irrelevant to the debate at hand, or both. Those familiar with taxonomic and evolutionary theory will see that by simply reading them. Others can get the flavor by considering the phrase "Were evolution a *static process*. . ." (our emphasis). Presumably what Miller and Brown mean is that evolution in different lines can proceed at different rates (a textbook discussion can be found in Ehrlich et al., 1974). If there have been significant rate differences in the lines leading to different groups of butterfly species (it is not known if there have been), this would not make one iota of difference in whether conservative nomenclature could be applied to the *products* of butterfly evolution.

It might be noted that the question of whether nomenclature should be conservative is not only independent of evolutionary rates but also of notions of what kinds of relationship should be the basis of taxonomic schemes. For example, Ehrlich and Ernst Mayr were on opposite sides of the phenetics vs. phyletics arguments of a quarter of a century ago, but they are in close agreement on keeping obligatory categories conservative.

12. From the comment on "political morality" we can only assume that Miller and Brown are more interested in conserving generic names than in conserving butterflies. We would claim that the only moral course (indeed the only sane one) is to use every available scientific and political tool at our disposal in attempts to save Earth's dwindling biological resources. This issue is explored in depth elsewhere (Soule and Wilcox, 1980; Ehrlich and Ehrlich, 1981).

13. Splitting and unsplitting genera, or the publication of catalogue/checklists, will not bring us any closer to a "true phylogenetic classification of the Lepidoptera." Even if "phylogenetic" is rigorously defined, a phylogenetic classification is not even necessarily the most desirable goal.

One might view this whole argument as scientifically trivial, but it is not. Sound nomenclature is important to evolutionists, ecologists, and other biologists as well as systematists. Butterflies are prominent organisms, fast becoming one of the most important groups of experimental animals. Confusing and senseless changes now will only impede scientific investigation, confuse serious amateur lepidopterists, and unnecessarily further lower the esteem of taxonomists in their colleague's eyes.

In summary, we state again that the Miller-Brown catalogue/checklist is, as a bibliographic tool, one of the most useful publications on North American butterflies ever to appear. In its introduction (p. v) we find that of the two authors "the elder [Brown]. . . favors the use of subgenera, the younger does not." It is too bad that Brown's mature taxonomic judgment did not prevail. It would be a shame if the resultant misuse of generic names were to be widely followed and thus cause the work to have an overall negative impact on science as a whole and the study of butterflies in particular.

Acknowledgments. We thank Carol L. Boggs, Richard W. Holm, John H. Thomas, Ward B. Watt, and Bruce A. Wilcox for reading and criticizing this manuscript.

Literature Cited

- BERENBAUM, M., 1978. Effects of linear furanocoumarins on an adapted specialist insect (*Papilio polyxenes*). *Ecol. Entomol.* 6:345-351.
- CHEW, F. S., 1977. Coevolution of pierid butterflies and their cruciferous foodplants II. The distribution of eggs on potential foodplants. *Evolution* 31:568-579.
- EHRlich, P. R., & A. H. EHRlich, 1981. *Extinction: The Causes and Consequences of the Disappearance of Species*. Random House, New York.
- EHRlich, P. R., R. W. HOLM, & D. R. PARNELL, 1974. *The Process of Evolution*, Second Edition. McGraw-Hill, New York.
- EHRlich, P. R. & D. D. MURPHY, 1982[1981]. Butterfly nomenclature: a critique. *J. Res. Lepid.* 20:1-11.
- HIGGINS, L. G., 1978. Aa revision of the genus *Euphydryas* Scudder (Lepidoptera: Nymphalidae). *Entomol. Gaz.* 29:109-115.
- HOLDREN, C. E., & P. R. EHRlich, 1982. Ecological determinants of food plant choice in the checkerspot butterfly *Euphydryas editha* in Colorado. *Oecologia (Berl.)* 52:417-423.

- JANZEN, D. H., 1979. New horizons in the biology of plant defenses. In G. A. Rosenthal and D. H. Janzen, eds. *Herbivores: Their Interaction with Secondary Plant Metabolites*. Academic Press, New York.
- LINCOLN, D. E., T. S. NEWTON, P. R. EHRLICH, & K. S. WILLIAMS, 1982. Coevolution of the checkerspot butterfly *Euphydryas chalcedona* and its larval food plant *Diplacus aurantiacus*: larval response to protein and leaf resin. *Oecologia (Berl.)* 52: 216-223.
- MAYR, E., 1969. *Principles of Systematic Zoology*. McGraw-Hill, New York.
- MILLER, L. D. & F. M. BROWN, 1981(82). Butterfly taxonomy: a reply. *J. Res. Lepid.* 20(4):193-198.
- MURPHY, D. D., 1983. Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). In press, *Envir. Ent.*
- RAUSHER, M. D., 1982. Population differentiation in *Euphydryas editha* butterflies: adaptation to different hosts. *Evolution* 36:581-591.
- SIMPSON, G. G., 1961. *Principles of Animal Taxonomy*. Columbia, New York.
- SINGER, M. C., 1972. Complex components of habitat suitability within a butterfly colony. *Science* 176:75-77.
- SOULE, M. C. & B. A. WILCOX, 1980. *Conservation Biology*. Sinauer and Co., Sunderland, Mass.
- WIKLUND, C., 1982. Generalist versus specialist utilization of host plants among butterflies. In press, *Proc. 5th Int. Symp. on Insect-Plant Relationships*, Wageningen.